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Water availability is more important than temperature in driving the carbon fluxes of an alpine meadow on the Tibetan Plateau

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ABSTRACT

Temperature is conventionally considered as the dominant factor regulating carbon fluxes of the alpine meadow on the Tibetan Plateau, while contribution from water availability is composed of large uncertainty. In this study, eddy covariance (EC) data were used to assess the relative contribution of temperature and water availability to carbon fluxes of the alpine meadow ecosystem. The results showed that soil water content (SWC) was the most important factor controlling carbon fluxes – Net Ecosystem Productivity (NEP), Gross Primary Productivity (GPP) and Ecosystem Respiration (Re). The GPP and Re increased with strengthened SWC under any temperature conditions, indicating the dominant control of water availability on carbon fluxes. In addition, water availability regulated the response size of ecosystem to temperature, and could alleviate the stress caused by low temperature. The photosynthesis capacity of alpine plants at noon was depressed by water stress rather than by high temperature. The structural equation modeling (SEM) analysis further confirmed the dominance of SWC on the carbon fluxes. This study implies that effects of climatic change on this alpine ecosystem might be more induced by changes in water pattern than increased temperature, which provides new insights into the climate controls of carbon fluxes over alpine meadow, and adds to our understanding on climate change impacts on carbon cycling on the Tibetan Plateau.

1. Introduction

Temperature and moisture are the two key factors regulating plant distribution and productivity (Epstein et al., 1997; Yu et al., 2013). Compared to increasing temperature, the precipitation trend varied strongly at temporal scales and spatial dimension on the Tibetan Plateau (Wang et al., 2008). The alpine ecosystems on the Tibetan Plateau are suggested to be highly sensitive to climatic change (Gao et al., 2009), but relative contribution from precipitation and temperature still involves much uncertainty (Craine et al., 2012). Disentangling their relative contribution to the carbon fluxes is the basis for understanding climatic variability impacts on the alpine ecosystems on the Tibetan Plateau.

Temperature affects plant growth and distribution (Sage and Kubien, 2007) via influencing physiological activities such as photosynthesis (Ganjurjav et al., 2015) and respiration (Hu et al., 2016). It is generally assumed that warming accelerates both photosynthesis and respiration (Wu et al., 2011). However, the acceleration magnitude varies in different ecosystems (Craine et al., 2012; Davi et al., 2007; Oberbauer et al., 2007). Also warming effects are adjusted by water availability (Wu et al., 2011; Yu et al., 2013). An ecosystem could shift from carbon source to sink when warming occurs along with increased precipitation (Harper et al., 2005). When warming occurs along with decreased precipitation, warming-induced soil drought could shift ecosystem from carbon sink to source (Ciais et al., 2005; Saleska et al., 2003).

Ecosystem productivity in cold environments is more responsive to warming than to cooling (Rustad et al., 2001), but carbon emission can also increase with warming owing to a greater sensitivity of respiration to warming (Lu et al., 2013). Altered precipitation has been suggested to exert larger impacts on semiarid ecosystems than on mesic ecosystems (Mooney et al., 1996). For example, the semiarid ecosystem productivity increased but that of the mesic one decreased under a similar annual precipitation of 380 mm (Sala et al., 2015).

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Regardless the critical role of water availability on ecosystem functions (Harper et al., 2005; Piao et al., 2007), most of previous studies have been focused on temperature effects on carbon fluxes of alpine meadow (Fu et al., 2009; Fu et al., 2006), whereas water availability played an even more important role in some cases (Wang et al., 2017a; Burke et al., 1997; Yang et al., 2009).

The alpine *Kobresia* meadow on the Tibetan Plateau is one of the highest-elevation vegetation types in the world (Wang et al., 2008), covering over $7 \times 10^5\,km^2$ and approximately 35% of the plateau. It is an extremely fragile system and highly sensitive to climatic change. Research findings for this system can be used as pre-warning for other low elevation ones (Zhang et al., 2013). Related knowledge is also critical for improving our prediction of global carbon cycle.

Alpine ecosystem is sensitive to both warming and cooling (Hu et al., 2016), but warming can cause no significant effects on GPP and aboveground biomass or its effect is regulated by water availability (Fu et al., 2013). Precipitation can change both photosynthesis and respiration (Angert et al., 2005; Breshears et al., 2005), but its net effects on carbon storage are still uncertain for the alpine ecosystem on the Tibetan Plateau (Zhang et al., 2016). To this end, eddy covariance and micrometeorological data were integrated to examine how carbon fluxes responded to climates. This work aimed at addressing the following questions: (1) How do climatic factors affect ecosystem carbon fluxes (GPP, Re and NEP)? (2) Are there interactions between temperature and water availability on carbon fluxes? (3) Between temperature and water availability, which one plays the dominant role?

2. Data and methods

2.1. Study site

The experimental site is located at 31.64°N, 92.01°E, 4598 m above sea level, in the hinderland of the Tibetan Plateau. The climate features the plateau subfrigid monsoon climate. The annual temperature averages −1.9 °C, with an active vegetation period length of 60–70 days. The annual precipitation is 380 mm, mainly concentrated in June–September and with large inter-annual variations. The annual average sunlight exceeds 2886 h. The soil is the meadow soil with sandy loam. The vegetation is typical alpine meadow, dominated by *Kobresia pygmaea*, accompanied by *Potentilla bifurca, Potentilla saundersiana, Leontopodium pusillum,* and *Carex moorcroftii*.

2.2. Instrumentation and measurements

The flux tower was located on a relatively flat open ground (< 3% slope in the primary wind direction). The open-path eddy covariance (OPEC) system, including a 3-D sonic anemometer (Model CSAT-3, Campbell Scientific Inc., Logan, UT, USA) to measure three-dimensional wind speed and temperature fluctuations, and an infrared gas analyzer (Model LI-7500A, Li-cor Inc., Lincoln, NE, USA) to measure carbon dioxide (CO_2) density, was used to measure carbon fluxes at 2.3 m above the ground. The flux data were collected at 10 Hz, then resampled to 30 min averages by a CR3000 datalogger (Model CR3000, Campbell Scientific).

The micrometeorological variables were measured near the OPEC system. Air temperature (Ta) and relative humidity (RH) were recorded at 1.8 m above ground by a temperature and humidity probe (Model HMP45C, Vaisala Inc., Helsinki, Finland), respectively. Photosynthetically active radiation (PAR) was measured at 1.5 m above the ground with a quantum sensor (LI190SB, Li-cor Inc.). Precipitation (PPT) was recorded at 1 m above ground level using a tipping bucket rain gauge (TE525MM-L, Campbell Scientific). Soil temperatures (Ts) and soil volumetric water contents (SWC) were measured at 0.05, 0.10, 0.20 and 0.50 m below the ground with thermometers (109-L, Campbell Scientific) and TDR probes (Model CS616-L, Campbell Scientific), respectively. The micrometeorological data were collected with a frequency of 1 Hz and then resampled to 30 min averages using a CR1000 datalogger (Model CR1000, Campbell Scientific).

2.3. Data processing

2.3.1. Eddy covariance data

The CO_2 flux data were processed using a data processing procedure for ChinaFLUX (Yu et al., 2006) implemented in Matlab R2010b software (MathWorks Inc., Natick, MA, USA). The flux data were first aligned with the coordinate system of mean wind direction using the three-dimensional rotation, to remove the effects of instrument tilt irregularity on the airflow (Wilczak et al., 2001). Then the WPL correction – the Webb, Pearman and Leuning density correction for effects of air density fluctuations on CO_2 fluxes – was used to adjust air density changes caused by heat and water vapor fluctuations (Webb et al., 1980). Missing or screened out data caused by power failures, instrumental malfunctions, and data filtering criteria such as the sonic temperature, water vapor density, CO_2 density values occurring outside reasonable bounds, rain, dew, hoarfrost, etc. were excluded from the analysis.

The CO_2 flux measured by the EC technique was the net ecosystem CO_2 exchange (NEE). There was a simple conversion of NEP = −NEE, then GPP could be estimated by GPP = NEP + Re, where Re is derived from the nighttime NEE (Reichstein et al., 2005). In order to eliminate the effects of poor turbulent mixing on nighttime CO_2 flux data, the data analyzed was restricted to the conditions when the friction velocity (u*) was greater than $0.14\,m\,s^{-1}$ (Saleska et al., 2003; Scott et al., 2006).

All flux and meteorological data collected were quality controlled. Data gaps were filled using the interpolation methods (Baldocchi, 2003) and the mean diurnal variation (MDV) method (Falge et al., 2001).

2.3.2. Data analysis

2.3.2.1. Vapor pressure deficit. The vapor pressure deficit (VPD) was calculated by the measurements of air temperature (Ta) and relative humidity (RH) (Howell and Dusek, 1995):

$$VPD = 0.611 \times e^{\frac{17.27 \times Ta}{Ta+237.3}} \times \left(1 - \frac{RH}{100}\right) \quad (1)$$

2.3.2.2. Anomaly analysis. The anomaly was calculated as the difference between the specific value of a given day and the corresponding multi-year average of that day to identify the variations of climatic factors and carbon fluxes of each day:

$$A_{doy,y} = F_{doy,y} - \frac{1}{5}\sum_{n=2012}^{2016} F_{doy,n} \quad (2)$$

where, A is the anomaly, F are daily values of carbon fluxes or climatic factors, doy = 1–365, y = 2012–2016.

2.3.2.3. Multiple stepwise regression analysis. Six main climatic factors (photosynthetically active radiation (PAR), air temperature (Ta), soil temperature (Ts), precipitation (PPT), vapor pressure deficit (VPD) and soil water content (SWC)) were selected and the multiple stepwise regression analysis between carbon fluxes and climatic factors were conducted with SPSS statistics 19.0 software (IBM Corporation, Armonk, NY, USA), aiming to identify the key climatic factors linked to carbon fluxes. The minimum P-value for a variable to be included or excluded from the model was 0.05. The higher F-value represents a better fit.

2.3.2.4. Trend - fitting analysis. The OriginPro 9.2 software (OriginLab Corporation, Northampton, MA, USA) was used to fit the generalized linear regression, exponential or logarithmic model of carbon fluxes against climatic factors. The better-fit functions that possess a higher r-

value and lower P-value were selected and their fitting curves were plotted. The poisson density function was employed to assess the relationship between GPP and Ta based on the 30 min data.

2.3.2.5. Temperature sensitivity (Q_{10}). The Re was first parameterized with a traditional Q_{10} model to fit the soil temperature at 5 cm depth as described by (Lloyd and Taylor, 1994) and (Falge et al., 2001):

$$Re = ae^{bTs} \quad (3)$$

where a and b are the regression coefficients, and a is the Re when soil temperature is 0℃. The respiration temperature sensitivity coefficient (Q_{10}) was determined as:

$$Q_{10} = e^{10b} \quad (4)$$

2.3.2.6. Structural equation modeling. The structural equation modeling (SEM) is a statistical methodology that can link climatic factors and carbon fluxes. It quantitatively describes the multivariate relations between covariates and dependent factor and can test the multivariate hypotheses. The overall purpose of SEM in this study was to examine the relative importance of the various climatic factors on carbon fluxes. The SEM was implemented with Amos 17.0.2 software (Amos Development Corporation, Crawfordville, FL, USA). We set climatic factors and carbon fluxes as observed variables. A "conceptual model" that considers the collinearity among climatic factors and effects of climatic factors on carbon fluxes was built. The fit indexes such as RMR (Root Mean Square Residual), GIF (Goodness of Fit Index), AGFI (Adjust Goodness of Fit Index), CFI (Comparative Fit Index), NFI (Normed Fit Index), IFI (Incremental Fit Index), RMSEA (Root Mean Square Error of Approximation), AIC (Akaike Information Criterion), BCC (Browne-Cudeck Criterion) and ECVI (Expected Cross-Validation Index) were employed to evaluate model fitness and whether the sign and strength of directional paths in SEM were appropriate.

3. Results

3.1. The dynamics of climatic factors and carbon fluxes

Climatic factors and carbon fluxes exhibited obvious seasonal dynamics (Fig. 1). Both radiation and temperature followed unimodal distributions. During the observation period, the mean annual Ts was 2.23 ℃, significantly higher ($P < 0.01$) than mean annual Ta (= −1.48 ℃). Their difference reached 3.71 ℃, crossing the biological boundary temperature of 0 ℃. The Ta averaged −11.62 ℃ during winter (from December to February of next year), and the mean Ts was −7.78 ℃. The minimum Ta during the observation period was −25.53 ℃ and appeared on January 10th, 2015. The minimum Ts was −13.78 ℃ and occurred next day. The Ts decreased sharply in October of 2013. Meanwhile, a sharp decrease in Re was identified.

The SWC varied with PPT. Because SWC decreased sharply under severe droughts in the growing season, the SWC followed bimodal distributions in 2013 and 2015. Especially in 2015, PPT amount was only 289 mm. The bimodal distribution in SWC directly caused the bimodal distributed carbon fluxes. The precipitation was abundant in 2014 and the SWC maintained a high level during the whole growing season. Thus, carbon fluxes in 2014 were higher than in other years. Low SWC in the early growing season resulted in low GPP in 2016, causing the ecosystem to be a carbon source. When the rainy season started, SWC increased rapidly, causing increased GPP, and the ecosystem turned into a carbon sink.

VPD is related to air moisture content, and also varied with PPT, but showed an opposite trend with SWC. In general, VPD followed a unimodal distribution with high value in growing season and low value in non-growing season. During the drought season with low PPT, SWC decreased and VPD increased. In rainy season, SWC increased and VPD decreased.

To identify the variations of climatic factors and carbon fluxes, the anomaly analysis was conducted (Fig. 2). The anomalies in PAR showed relatively similar fluctuations among the observation years. Except for 2015, severe water shortage occurred during the active and later growing season. During the two periods, the anomalies in PAR and VPD remained positive, while the anomalies in PPT and SWC were negative. During the drought periods, low PPT and strong PAR resulted in water stress and the negative carbon fluxes anomalies. The carbon fluxes were substantially influenced by water stress during active growing seasons, but little impacted during the later growing season. In addition, drought also occurred in growing season of 2013, causing negative anomalies in PPT, SWC and carbon fluxes, while positive anomalies in VPD. In 2014, the SWC anomalies were mostly positive, causing positive carbon fluxes anomalies in this year. The changes of SWC anomalies were consistent with that of carbon fluxes anomalies, and approximately opposite to that of VPD anomalies.

The continuous negative anomalies in Ta occurred in later 2013, and the negative anomalies in Ts were large over the same period. However, the anomalies in Ta and Ts were positive in early 2014. Thus, the carbon fluxes in 2014 were not influenced by the low temperature at the end of 2013. In 2015, the anomalies in Ts were always positive due to drought and Ts was always at a high level. The anomalies in Ta and Ts were almost positive in the latter part of 2016.

3.2. Climatic drivers of carbon fluxes

The top three best-fitted equations were screened by the multiple stepwise regression analysis (Table 1). The results showed that both NEP and GPP could be represented by SWC, Ts and PAR, and representation by SWC alone would be best (for NEP: $F = 52.5$, $P < 0.01$; for GPP: $F = 96.7$, $P < 0.01$). Re could be represented by SWC, Ts and VPD. SWC and Ts in combination explained the highest proportion of Re variations ($F = 80.2$, $P < 0.01$). In general, SWC and Ts explained a higher proportion of carbon fluxes variations than VPD, Ta and PPT did. The correlations between SWC and carbon fluxes were highest in each model, which further confirmed that SWC dominated the variations of carbon fluxes.

3.3. SWC effects on GPP and Re

To improve the estimation accuracy, observed half-hourly data of growing season from 2012 to 2016 were screened to estimate the optimum temperature for productivity of the alpine meadow. Fig. 3 clearly showed that GPP increased slowly when Ta < 5℃, and maintained a high level when Ta > 8℃, then started to decrease when air temperature was over 12.2 ℃.

The effects of SWC on GPP and Re were investigated based on the optimum temperature analysis results with the thresholds of 5 ℃ and 8 ℃ (Fig. 4). GPP and Re increased with enhanced SWC under any temperature conditions. In the range of Ta < ℃, GPP and Re increased exponentially with elevated SWC. In the range of 5 ≤ Ta < ℃, GPP increased linearly and Re increased logarithmically as SWC strengthened. In the range of Ta ≥ 8 ℃,GPP increased exponentially and Re increased linearly with improved SWC.

3.4. SWC effects on the responses of GPP and Re to Ts

Fig. 5 demonstrated the interaction effects of soil temperature and moisture on carbon fluxes. The effects of Ts on GPP and Re were greatly influenced by SWC. With increased SWC, the sensitivities of GPP and Re to Ts strengthened. Ts had little impacts on GPP ($P = 0.2$) when SWC < 0.07 $m^3 m^{-3}$. That is to say, under drought stress, the productivity was still low even under suitable temperature conditions. GPP increased rapidly (slope = 0.15) as Ts increased when 0.07 ≤ SWC < 0.14 $m^3 m^{-3}$, and then increased at a higher rate (slope = 0.32) at SWC ≥ 0.14 $m^3 m^{-3}$, meaning that GPP increased

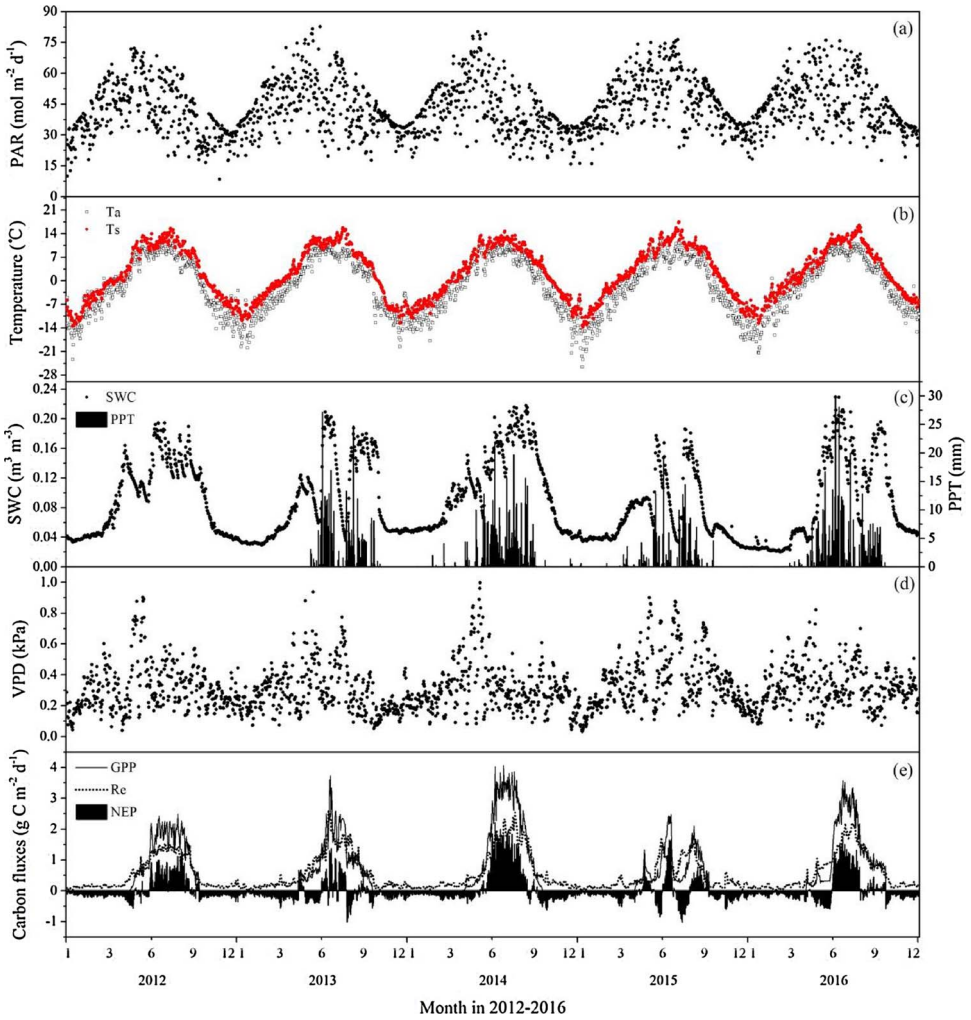

Fig. 1. Daily values of climatic factors and carbon fluxes during 2012–2016. Precipitation (PPT) data were available since June 2013; both Ts and SWC were collected from a soil depth of 0.05 m.

rapidly with increasing Ts as long as the moisture conditions were favorable (SWC ≥ 0.07 $m^3 m^{-3}$). Re increased exponentially with increased Ts ($P < 0.01$) under any SWC conditions. Re increased slowly ($Q_{10} = 1.92$) as Ts increased when SWC < 0.07 $m^3 m^{-3}$, and then increased at a rapid rate ($Q_{10} = 2.55–2.58$) when SWC ≥ 0.07 $m^3 m^{-3}$. It underlay that low SWC could inhibit the sensitivity of Re to Ts.

3.5. SWC dominated carbon fluxes

To further demonstrate the key role of moisture conditions, the main controlling environmental factors (including Ts, PAR, VPD and SWC) were selected to build the structural equation modeling.

As shown in the Table 2, RMR and RMSEA were close to 0; GFI, AGFI, CFI, NFI and IFI were close to 1; AIC, BCC and ECVI were lower than the corresponding values of Saturated model and Independence model. These indicated that the model was a perfect fit.

The standardized coefficient value representing effects of SWC on GPP was 0.63 (Fig. 6), greater than that of Ts on GPP (SC = 0.37). The Re was under the joint control of SWC and Ts, and their SCs were 0.57 and 0.58, respectively. The VPD was negatively related to GPP and Re. The SC representing total effects of PAR on GPP was 0.20, revealing marginal effects from PAR in the alpine region.

4. Discussions

4.1. Seasonal patterns of climatic factors and carbon fluxes

The seasonal patterns of carbon fluxes are consistent with the plant growth dynamics (Xu and Baldocchi, 2004). Temperature is the dominant factor controlling start and end of growing seasons (Kato et al., 2006; Rollinson and Kaye, 2012; Xu et al., 2005). As a result, the seasonal patterns of carbon fluxes are mainly controlled by seasonal patterns of temperature (Körner and Basler, 2010; Saito et al., 2009).

The growing season in this study site lasts from June through September. Both July and August are the active vegetation period (Zhang et al., 2015b), when solar radiation and temperature variations are not pronounced (Fig. 1a,b), but significant for moisture (Fig. 1c,d; Zhang et al., 2015a). Therefore, water availability can be the most limiting factor on carbon fluxes during growing seasons. Limited precipitation and low soil moisture during the growing seasons are the primary climatic factors limiting CO_2 gains in the alpine meadow ecosystem targeted in this study (Fig. 2; Ferlan et al., 2016). The GPP and NEP anomalies decrease with PPT and SWC, also exhibit negative anomalies in growing season. Similar findings have been reported for a mesic tallgrass prairie ecosystem in northeastern Kansas (Fay et al., 2000; Harper et al., 2005).

Seasonal variations of carbon fluxes are limited by low temperature during non-growing seasons (Kato et al., 2006), which in turn are regulated by water availability during growing seasons (Goodrich et al.,

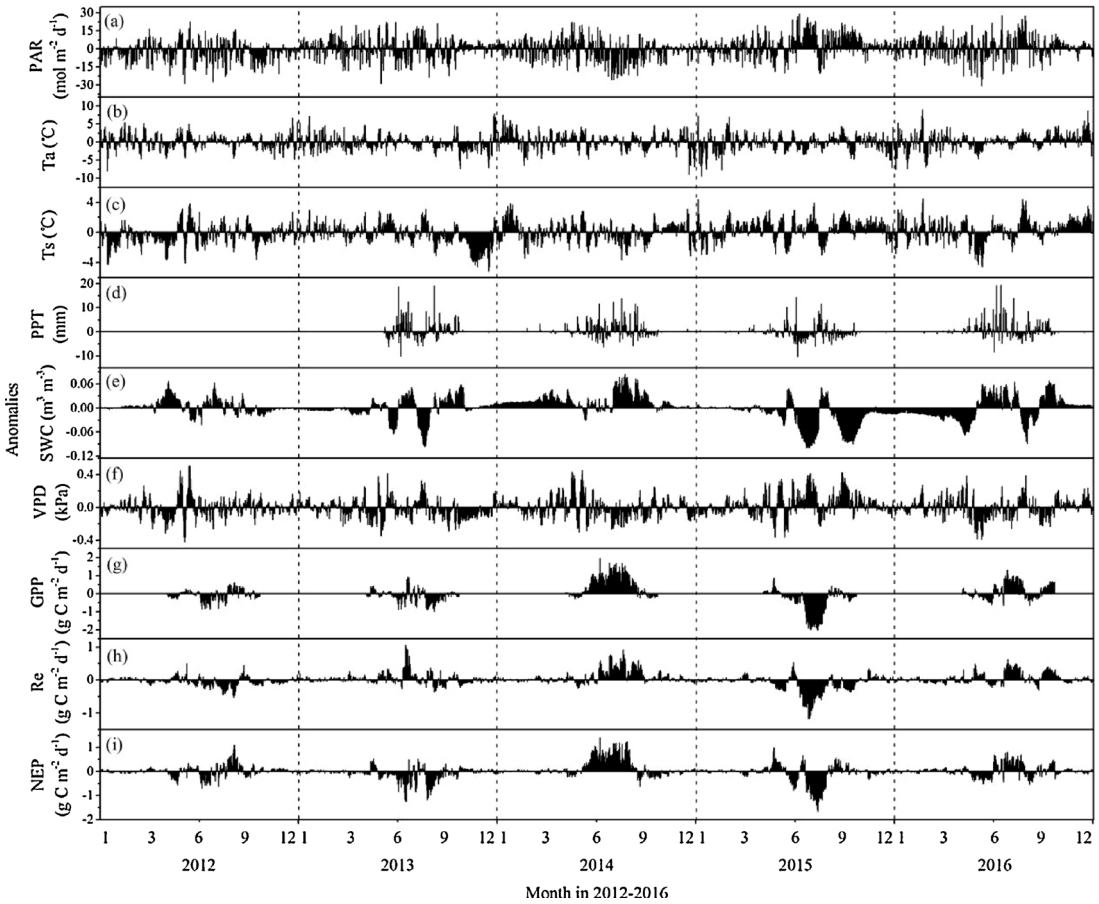

Fig. 2. Daily anomalies of climatic factors and carbon fluxes from 2012 to 2016. Precipitation (PPT) data were available since June 2013.

2015; Xu and Baldocchi, 2004), especially in drought year (Hunt et al., 2002). In the extreme drought year of 2015, the carbon fluxes dynamics was in accord with SWC patterns (Fig. 1c,e). The moisture limitation strengthens in early spring with rising temperature (Ganjurjav et al., 2016), and can delay vegetation greening when precipitation is inadequate (Wang et al., 2017b). Carbon exhibits high fluxes mainly in growing season (Kato et al., 2006), as being accounted for largely by SWC (Gao et al., 2012). Therefore, it can be generalized that the total annual carbon fluxes of dry and semi-dry ecosystems are primarily controlled by SWC (Luan et al., 2016).

4.2. Overestimated effects of low temperature stress

Environmental factors, including solar radiation, temperature, precipitation, soil moisture and VPD, all affect ecosystem carbon cycle to some extent (Fu et al., 2009). For this alpine meadow ecosystem, SWC and Ts, rather than PPT or Ta, are the main driving factors (Table 1), indicating that soil temperature and moisture exert more direct effects on vegetation compared with air environment (Shi et al., 2006; Xue et al., 2014).

Furthermore, the mean annual Ta in this alpine ecosystem is below 0 ˚C, but the mean annual Ts is above 0 ˚C – the agricultural threshold temperature, which is critical for vegetation growth and would make a great influence on ecosystem (Bheemanahalli et al., 2016; Saito et al., 2009). In winter, air temperature decreases sharply, while soil temperature decreases in a relatively gradual mode (Fig. 1b), which provides safe conditions for vegetation going through winter (Ichizen et al., 2002). Therefore, low temperature stress might not be the most limiting factor on the alpine plants if the determining factor is soil temperature instead of air temperature (Mcmaster and Wilhelm, 1998). This finding

Table 1
The results of multiple stepwise regression analysis of carbon fluxes (NEP, GPP and Re) against the potential drivers (PAR, Ta, Ts, PPT, VPD and SWC) during the active vegetation period from 2012 to 2016. The Ts, PAR, VPD and SWC columns represented the partial correlation coefficients between carbon fluxes and each climatic factor, respectively.

stepwise regression equation	F	P	Ts	PAR	VPD	SWC
NEP = −0.165 + 5.181SWC	52.5	< 0.01	–	–	–	0.36**
NEP = −0.955 + 6.688SWC + 0.012PAR	38.8	< 0.01	–	0.26**	–	0.43**
NEP = −1.475 + 7.3SWC + 0.01PAR + 0.044Ts	27.1	< 0.01	0.10*	0.19**	–	0.43**
GPP = 0.772 + 8.87SWC	96.7	< 0.01	–	–	–	0.47**
GPP = −2.047 + 12.603SWC + 0.189Ts	79.1	< 0.01	0.35**	–	–	0.56**
GPP = −2.117 + 12.884SWC + 0.172Ts + 0.01PAR	53.6	< 0.01	0.30**	0.10*	–	0.56**
Re = 0.936 + 3.689SWC	71.2	< 0.01	–	–	–	0.41**
Re = −0.714 + 5.874SWC + 0.111Ts	80.8	< 0.01	0.42**	–	–	0.56**
Re = −0.692 + 5.038SWC + 0.139Ts-0.665VPD	60.2	< 0.01	0.45**	–	−0.19**	0.47**

* indicates that the correlation is significant at the 0.05 level.
** indicates that the correlation is significant at the 0.01 level.

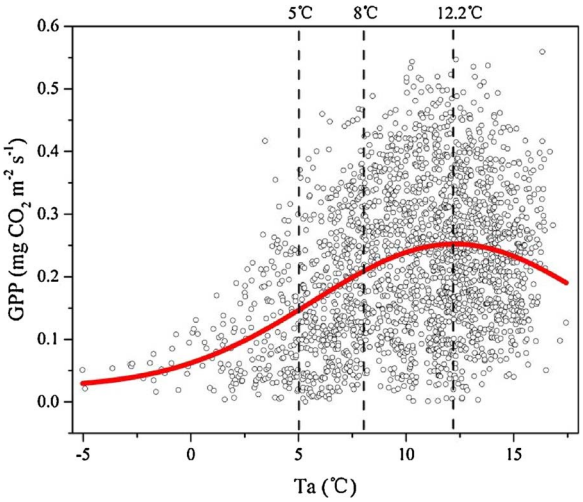

Fig. 3. The relationship between GPP and air temperature (Ta). The curve was fitted based on the 30 min data of growing season from 2012 to 2016.

challenges previous findings that low temperature overwhelmingly limits ecosystem functions of the alpine vegetation (Fu et al., 2006; Kato et al., 2006; Saito et al., 2009).

4.3. Moisture regulated responses of ecosystem carbon fluxes to temperature

On the Tibetan Plateau, temperature has been increasing at a rate above the Northern hemisphere average, and precipitation has also enhanced (Zhang et al., 2013). The rapid climate change adds to the complexity of understanding climate effects on carbon fluxes of alpine grasslands. Prior studies showed that temperature and moisture are the main driving forces on ecosystem carbon fluxes (Yu et al., 2013), and their combined effects are predicted to have stronger influences (Barron-Gafford et al., 2012; Powell et al., 2006). The low temperatures generally restrict plant production in cold environments (Hudson et al., 2011). However, this study found that SWC plays a more important role in carbon fluxes of the alpine ecosystem.

Increased SWC directly promotes GPP and Re, even under low Ta conditions (Fig. 4a,d). The reason might be that SWC could effectively alleviate side effects of low Ts due to water's large heat capacity (Anderson and Mcnaughton, 1973). So, suitable SWC might alleviate the low temperature stress and maintain high values of GPP and Re (Wen et al., 2006). However, even under suitable temperature conditions, GPP and Re are significantly suppressed as long as SWC is low (Fig. 5), indicating the absolute controlling force stemmed from SWC (Luan et al., 2016). Therefore, water stress is potentially more harmful to the alpine ecosystem than low temperature stress in terms of ecosystem productivity (Riveros-Iregui et al., 2007).

The SWC modifies the effect size of Ts on carbon fluxes (Xue et al., 2014). The sensitivities of GPP and Re to Ts strengthen with increased SWC (Fig. 5; Zhang et al., 2010). This result implies that the extrapolation of alpine meadow carbon fluxes to the future climates based on a constant temperature sensitivity would create a significant bias. However, the responses of GPP and Re to SWC are not restricted by temperature (Fig. 4). Taken together, SWC plays a key role in affecting carbon fluxes (Ganjurjav et al., 2016). Increased SWC also enhances GPP at a faster rate than on Re (Fig. 4), which indicates that sensitivity of GPP to SWC is greater than that of Re (Yu et al., 2013). In addition, SWC determines NEP to a greater extent (Table 1). These conclusions are complementary to the previous studies from the point of view of water sensitivity, i.e. compared to Re, GPP is a primary driver on NEP (Larsen et al., 2007; Zhang et al., 2016).

This study focused on the carbon fluxes of alpine meadow, the dominating ecosystems on the Tibetan Plateau, and showed that soil moisture regulates the response of carbon fluxes to temperature, which further confirmed and extended the previous broad-scale studies results (Wang et al., 2013; Wang et al., 2014; Wang et al., 2017b). The alpine meadow ecosystem carbon fluxes are not only subject to temperature, but are also subject to water availability (Yu et al., 2013). Especially during dry season, moisture supply would be the key factor limiting carbon fluxes (Wang et al., 2013). When below a threshold of water limitation, SWC would limit any temperature-driven increase in carbon fluxes even during a warmer period (Angert et al., 2005). Drought-

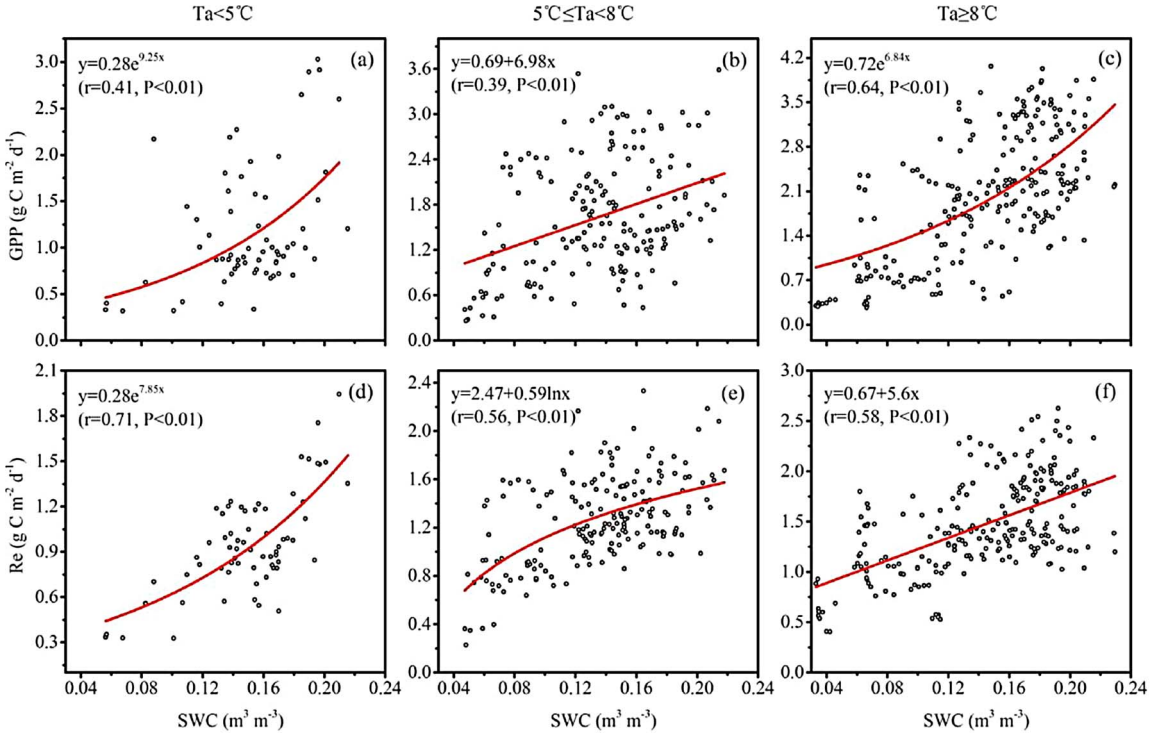

Fig. 4. The relationships between carbon fluxes (GPP and Re) and soil water content (SWC) under different air temperature (Ta) during the active vegetation period from 2012 to 2016.

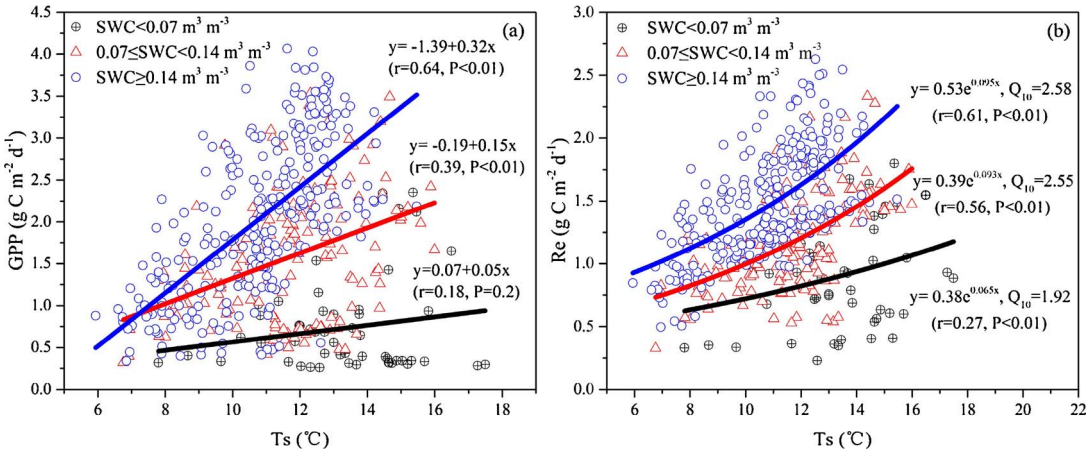

Fig. 5. The relationships between carbon fluxes (GPP and Re) and soil temperature (Ts) under different soil water content (SWC) during the active vegetation period from 2012 to 2016.

induced reduction in photosynthesis might result in a larger CO_2 emission to the atmosphere (Schwalm et al., 2011), because photosynthesis usually decreases more than respiration during drought (Wang et al., 2014). Temperature would become increasingly important during wet season (Wang et al., 2017b), because the sensitivities of carbon fluxes to temperature would strengthen with increasing SWC, when mixed climatic controls on carbon fluxes (Barron-Gafford et al., 2012; Sala et al., 2015).

4.4. Water stress depressing photosynthesis

The alpine plants on the Tibet Plateau have adapted to the long-term low temperature conditions, and their photosynthetic could be depressed at relatively high temperature (Cui et al., 2003). Previous studies have suggested that photosynthesis of alpine plants is usually depressed at noon under high temperature (Fu et al., 2006; Li et al., 2006). As found in this study, the water stress under high noon temperature might be the main limiting factor causing photosynthetic depression.

To further illustrate the underlying environmental mechanism behind drought depressed photosynthesis, a comparison of diurnal courses of GPP and relevant environmental factors for well watered and severe drought conditions was conducted (Fig. 7). The GPP in drought months were significantly ($P < 0.01$) lower than that in wet months (Fig. 7q–t), and the differences of SWC and VPD between drought and wet months were greater than those of PAR and Ts (Fig. 7a–p). This comparison further indicates that moisture conditions, particularly SWC (Fig. 7i–l), are the primary reason causing decreased GPP, which is in accord with other similar studies on the alpine system (Luan et al., 2016).

The night temperature is low on the northern Tibet Plateau and lots of dew are condensed in the morning, which creates favorable conditions of SWC and VPD and improves ecosystem productivity during the forenoon (Fig. 7i–t). After sunrise, the effects of dew gradually disappeared and VPD increased rapidly (Fig. 7m–p). GPP peaked at 12:00 and decreased in the afternoon (Fig. 7q–t). The process of GPP decreasing could be divided into two stages: (1) During 12:00–18:00, VPD continued to rise and SWC decreased in wet months, and water shortage leaded to declined GPP; (2) GPP decreased rapidly after 18:00 because of low radiation. The reason why photosynthesis was depressed in

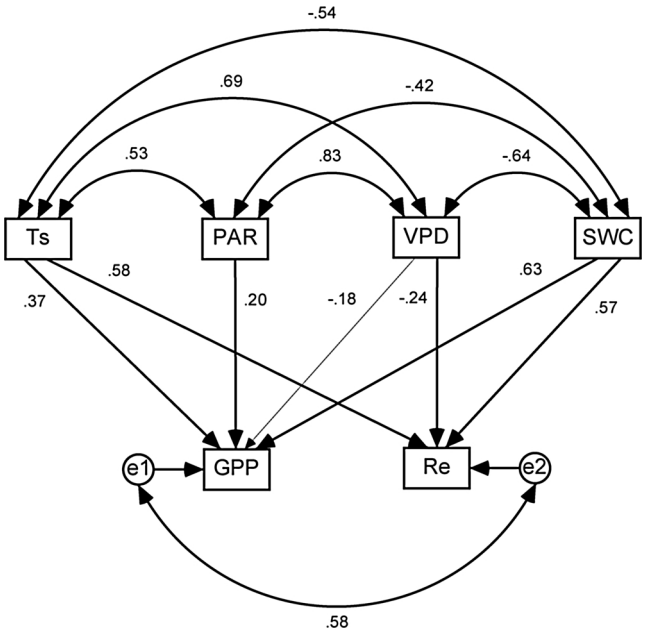

Fig. 6. Path diagram reflecting overall effects of main climatic factors on GPP and Re. The best-fit model resulted from structural equation modeling (SEM). Values on arrows were standardized coefficients (SC), representing standardized total effects of climatic factors on carbon fluxes. The bold arrows indicated statistically significant paths at $P \leq 0.01$. The thin arrows indicated nonsignificant paths.

drought months might be that water stress caused stomatal closure by decreasing expansion of guard cell (Goodrich et al., 2015), and inhibiting photosynthetic enzyme activities (Kim and Verma, 1990). Decreased SWC after noon in wet months but increased SWC in drought months (Fig. 7i–l) lent further evidence related to stomatal closure inhibited transpiration (Fu et al., 2006). It is thus clear that the alpine plants suffer from photosynthetic depression at noon due to water shortage in wet seasons, but water-induced stomatal closure is the driver responsible for GPP reduction in dry seasons (Tuzet et al., 2003). The distinct mechanisms behind the photosynthetic depression suggest the shifts of dominant factors on ecosystems under varying environmental conditions (Zhang et al., 2016).

Table 2
The indexes employed to evaluate model fittness.

Fit Index	RMR	GFI	AGFI	CFI	NFI	IFI	RMSEA	AIC	BCC	ECVI
Value	0.034	0.999	0.989	1	1	1	< 0.001	40.522	41.350	0.117

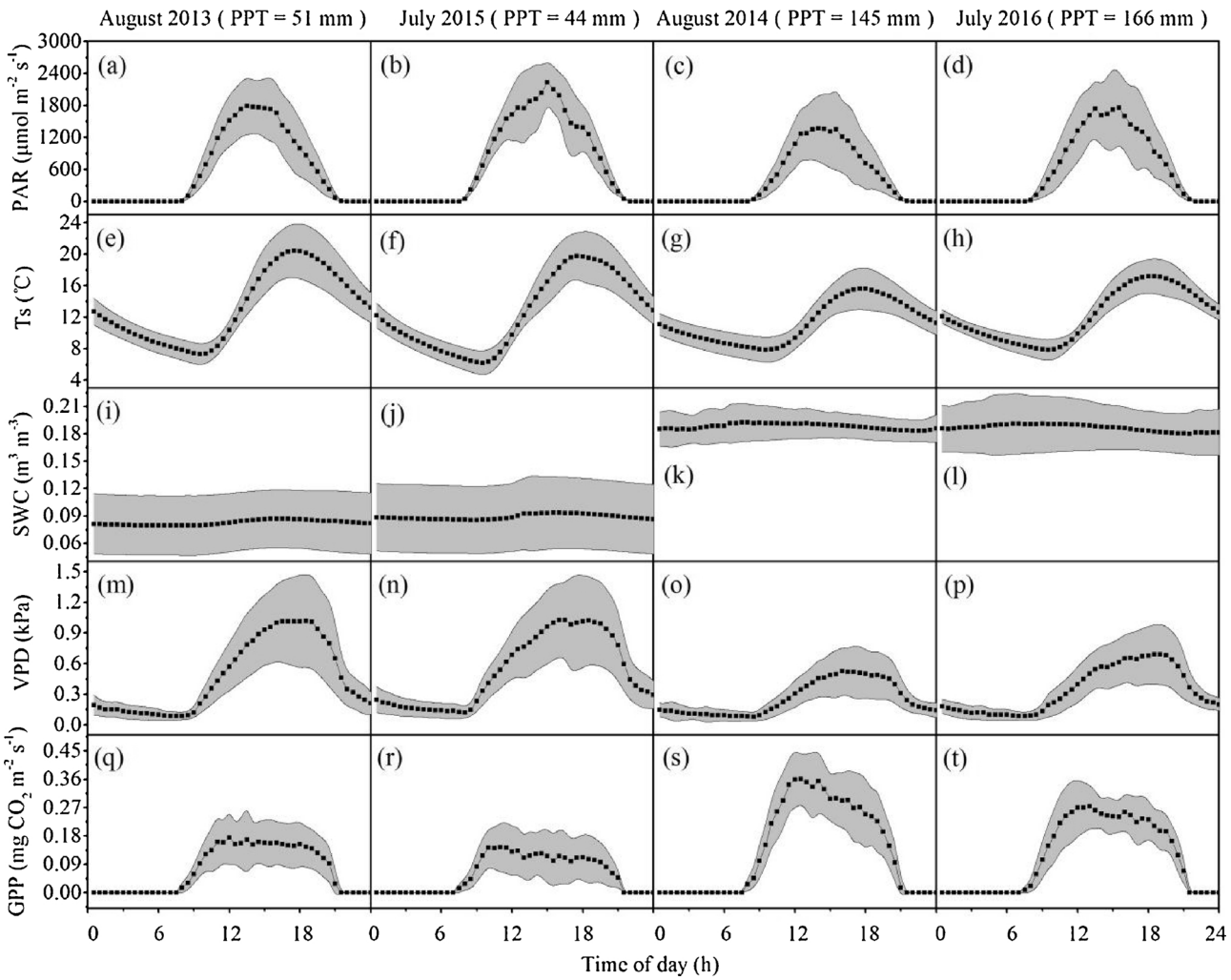
August 2013 (PPT = 51 mm)
July 2015 (PPT = 44 mm)
August 2014 (PPT = 145 mm)
July 2016 (PPT = 166 mm)
PAR (μmol m-2 s-1)
Ts (℃)
SWC (m3 m-3)
VPD (kPa)
GPP (mg CO2 m-2 s-1)
Time of day (h)

Fig. 7. Daily variations of the monthly means of PAR, Ts, SWC, VPD and GPP. The 30 min data are means for all days in each month, of which August 2013 and July 2015 belong to typical drought month. The water supplies in August 2014 and July 2016 are adequate. The shadow regions represent the standard deviation.

The water stress under high temperature of noon is suggested to be the main limiting factor inducing photosynthetic depression. By contrast, the importance of moisture in driving carbon fluxes would not be evident during nighttimes. This result is consistent with the previous study showing that there are asymmetric effects of daytime and nighttime temperature on northern hemisphere vegetation (Peng et al., 2013; Tan et al., 2015). The temperature sensitivities of carbon fluxes are regulated by SWC (Fig. 5). The differences of SWC between daytime and night-time would lead to a change in response of vegetation to temperature, which might be one reason for explaining the mechanism of this asymmetric effect. Furthermore, plant photosynthesis usually occurs during daytime and respiration occurs throughout the day (Atkin et al., 2013). Altered carbon flux composition from day to night could also cause the changing of responses of carbon fluxes to climatic factors. The consequent view of carbon flux is that ecosystem respiration is greater during the day than at night, which is in accord with our previous study in this site (Zhang et al., 2015b). However, a new research was conducted in a temperate deciduous forest ecosystem using a new isotopic instrumentation showing that the respiration is lower during the day than at night due to the inhibition of leaf respiration by light (Wehr et al., 2016), which therefore challenges the traditional NEE decomposition method.

4.5. Water availability dominated ecosystem carbon fluxes

Dry conditions could cause plant stress and lowered stomatal conductance (Sonnentag et al., 2010), and this physiological response would constrain ecosystem CO_2 exchange (Goodrich et al., 2015). The high VPD represents the low moisture content in the air. VPD was negatively correlated with Re (STE = −0.24) but no significant relationship was found with GPP (P = 0.065) in this study (Fig. 6).

In this alpine ecosystem, GPP is mainly affected by SWC (STE = 0.63) and slightly affected by Ts (STE = 0.37), and Re is jointly affected by SWC (STE = 0.57) and Ts (STE = 0.58) (Fig. 6), which is consistent with the results of the multiple linear stepwise regression analysis (Table 1) and previous studies (Fu et al., 2009; Ganjurjav et al., 2016). In addition, NEP is regulated more by GPP than by Re (Yu et al., 2013; Zhang et al., 2016). So, the effect of Ts on NEP is weakened (Table 1), and the role of SWC is strengthened (Riveros-Iregui et al., 2007). The landscape scale results of this study are in accord with other studies conducted on broad scales (Breshears et al., 2005; Craine et al., 2012; Gao et al., 2009; Wang et al., 2013; Wang et al., 2017b) and further prove the carbon fluxes in this alpine meadow might be regulated more by water availability than by temperature (Ganjurjav et al., 2016).

5. Conclusions

The variations in carbon fluxes are governed by water availability during growing seasons. Water availability directly affects carbon fluxes of the alpine ecosystem, also indirectly affects carbon fluxes through adjusting responses of ecosystems to temperature and

regulating stomatal behavior. Suitable moisture could alleviate the low temperature stress, but photosynthesis and respiration are significantly suppressed as long as moisture is low. Diurnally, photosynthesis of alpine plants at noon is depressed by water stress rather than by high temperature. Water shortage depresses photosynthetic capacity at noon in wet seasons, and water-induced stomatal closure is the mechanism underlying GPP reduction in dry seasons.

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